

A new species of fungus-growing ant and its implications for attine phylogeny (Hymenoptera: Formicidae)

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Abstract. *Apterostigma megacephala*, a new species of attine ant, is described from Peru and Colombia. It is diagnosed by the following combination of worker characters: flattened compound eyes partially wrapped around conical tubercles, mesonotal denticles and erect rigid pilosity on the head, mesosoma and gaster. It is thought to be a basal species in relation to the rest of *Apterostigma*. Phylogenetic relationships among basal genera of the tribe Attini are discussed.

Introduction

The Attini is a tribe of mostly Neotropical ants characterized by fungus-growing habits. They apparently constitute a monophyletic group as evidenced by this unique habit, and the larval morphology (Schultz & Meier, 1995), although the fungi themselves are polyphyletic (Chapela, 1994). Attines have been the object of many studies, but most of the work has been limited to groups of immediate economic importance such as *Atta* and *Acromyrmex*, leaving the other genera in relative obscurity. This dearth of information covers not only their ecology, but their taxonomic status as well, consequently making most of them difficult to identify. It is commonly agreed among myrmecologists that a confusing situation exists in the nature of the genera as they presently exist in the tribe, and that the relationships between these groups are unclear. Kusnezov (1964) delimited *Myrmicocrypta*, *Apterostigma* and *Mycocarpus* as a group called Palaeoattini within Attini. He argued for their more primitive status as compared with the rest of attines because of the characteristics of their nests and fungus gardens, fungal substrate, worker monomorphism and behaviour (Kusnezov, 1955). At least some of his conclusions have found support in studies of attine phylogeny based on larval morphology (Schultz & Meier, 1995). Their results corroborate the monophyly of the tribe, but render the genus *Myrmicocrypta* paraphyletic. *Myrmicocrypta buenzlii* apparently conserves the greatest number of ancestral attine characters. It forms a basal trichotomy, along with the clade formed by *Mycocarpus* and *Apterostigma* and the rest of the Attini.

During the course of gathering material for a revision of the genus *Apterostigma* (Lattké, 1997), specimens were found that

initially were considered a different genus. Subsequent work revealed them to be a basal *Apterostigma* with an unusual combination of characters that provide clues for the basal phylogeny of the Attini.

Materials and methods

Measurements and indices

- HL, Head length. The maximum straight-line distance from the posterior cephalic margin to the anterior clypeal margin with the head in full dorsal (frontal) view.
- HW, Head width. The maximum straight-line distance between the lateral cephalic margins, excluding the ocular prominences. Taken in the same plane of view as HL.
- LW, Frontal lobe width. The maximum straight-line distance between the external margins of the frontal lobes. Taken in the same plane of view as HL.
- ML, Mandibular length. The maximum straight-line distance between the outer mandibular base to the mandibular apex. Taken in the same plane of view as HL.
- SL, Scape length. The maximum straight-line distance of the first antennal segment measured from the basal constriction to the scape apex. This was taken in an oblique posterior cephalic view since the frontal lobes cover the antennal base in frontal view.
- CI, Cephalic index: HW/HL.
- SI, Scape index: SL/HW.

Collections

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UNCB, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Santafé de Bogotá, Colombia.

MCZC, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.

MIZA, Museo del Instituto de Zoología Agrícola, Universidad Central de Venezuela, Maracay, Aragua, Venezuela.

Phylogenetic relations

In an effort to gain an idea of the possible relationships of *Apterostigma megacephala* with other basal Attini, selected species from several genera were compared: *Apterostigma auriculatum*, *A. dentigerum*, *A. cf. pilosum*, *A. urichii*; *Blepharidatta brasiliensis*; *Mycocepurus goeldii*, *M. smithi*, *M. tardus*; *Myrmicoecrypta buenzi*; *Sericomyrmex amabilis*, *S. cf. saussurei*, *S. zacapanus*, *S. sp. 1*, *S. sp. 2*. *Blepharidatta*, a nonattine and putative sister group to Attini (Schulz & Meier, 1995) was included for determining character polarities. The following characters were used to determine relationships.

1. *Anterior strip of smooth and shiny integument on clypeus*: (0) absent; (1) present.

Table 1. Character state matrix for selected genera of Attini.

Taxon	Character							
	1	2	3	4	5	6	7	8
<i>Blepharidatta</i>	0	0	0	0	0	0	0	0
<i>Mycocepurus</i>	1	1	0	0	1	1	0	1
<i>Apterostigma</i>	—	0	1	1	1	0	1	1
<i>Myrmicoecrypta</i>	1	1	0	0	1	1	0	0
<i>Apterostigma</i>	1	1	1	1	1	1	1	1
<i>Sericomyrmex</i>	1	0	0	0	0	1	0	1

2. *Clypeus*: (0) without a ridge between it and the cephalic dorsum; (1) posterolaterally bound on each side by a ridge that extends from the frontal lobes and separates it from the antennal fossae and the rest of the cephalic dorsum.
3. *Compound eye*: (1) partially or totally supported on a tubercle; (0) ocular tubercle absent.
4. *Head*: (1) with a posterior ridge or lamella that joins the occipital lobes; (0) this structure absent.
5. *Lateral margins of pronotum*: (1) evenly curved, without a denticle or angle; (0) with a denticle or angle.
6. *Mesonotum*: (1) with two pairs of denticles; (0) without denticles.
7. *First gastral tergite*: (0) without an anterodorsal lobe that partially overlaps the helcium; (1) with this lobe.
8. *Carina along the lateral margins of first gastral tergite*: (0) absent; (1) present.

The character matrix (Table 1) was processed using the exhaustive search option of PAUP 3.1.1, which produced three trees, and from these trees the strict consensus tree shown in Fig. 5.

Apterostigma megacephala, sp.n (Figs 1–3)

Worker Diagnosis. Flattened compound eyes partially wrapped around conical tubercles, ommatidia reduced; mesonotal denticles present; erect rigid pilosity present on head, mesosoma and gaster; erect hairs with spatulate apices frequently present on mesosoma.

Holotype. PERU, Madre de Dios, Cuzco Amazónico, 15 km NE Puerto Maldonado, Río Tambopata, 200 m, 21-VI-89, S.P. Cover, J.E. Tobin, leg. CA-357. Plot IE 24. Worker deposited in MCZC.

Paratypes. (1) PERU, Madre de Dios, Estación Pakitza-



Fig. 1. Lateral view of body of *Apterostigma megacephala*. Extremities and pilosity omitted. Bar = 1.0 mm.

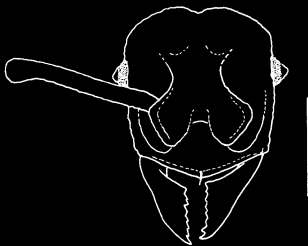


Fig. 2. Dorsal view of head of *Apterostigma megacephala*. Bar = 1.0 mm.

Manu, 13–17/02/92, R. Combra, D. Quintero leg. Worker deposited in CPDC. (2) COLOMBIA, Meta, Parque Natural La Macarena, IX-90, M.T. Barreto leg. Worker deposited in UNCB. (3) PERU, Madre de Dios, Manu Reserve Zone, Pakitza Station, X-88, J. Tobin leg. Worker deposited in MIZA.

Worker. Measurements, holotype (UNCB–CPDC paratypes): HL 1.69 (1.70–1.64); HW 1.44 (1.51–1.46); LW 0.90 (0.94–0.91); ML 0.90 (1.06–1.02); SL 1.47 (1.64–1.54); LM 2.49 (2.51–2.47) mm. CI 0.85 (0.89–0.89); SI 1.02 (1.09–1.05). Head in frontal view subquadrate, anterior clypeal border broadly convex, medially bluntly angulate or with blunt short denticle (Fig. 3); sides slightly diverging posterod, posterolaterally convex and with straight posteromedian border. Clypeus anteriorly with narrow, longitudinal band of smooth and shiny integument, remainder opaque, rugose; prominent median seta usually present on anterior edge, thicker and longer than surrounding hairs (Fig. 3). Clypeus medially with carinae forming Y-shaped ridge, each posterior arm stems from below frontal lobe, with anterior arm extending to posterior edge of shiny strip. Clypeus posterolaterally bound by ridge extending from frontal lobe, separating it from antennal fossae; each ridge then extends posterad, bordering antennal fossa laterally and joining rugae on cephalic dorsum just below level of eye. Frontal lobes relatively massive and subtriangular, with bluntly rounded apex, very short anterior margin, very broadly convex lateral margin and approximately straight posterior margin; dorsal surface with coarse longitudinally arching rugae. Frontal carinae extending posterad only to upper level of eyes, afterwards joining 2 posteromedian swellings that meet at midline to enclose dorsomedian cephalic depression. Compound eye on subconical tubercle, in lateral view forming ellipse curved around anterior half of tubercle; ommatidia flat, separated from one another. Occipital lobes short, subquadrate, joined by posterodorsal low transverse ridge. Cephalic sculpturing opaque, coarsely rugose except finely granulose



Fig. 3. Anteromedian clypeal area and inner posterior mandibular corners. Median clypeal seta visible as the most robust hair present.

antennal fossae, ocular prominences and most of dorsomedian depression. Scapes transversely rugose, base strongly bent, with rigid decumbent hairs. Antennal fossae relatively large, reniform. Dorsal mandibular surface striate, smooth and shiny along chewing border and distad; chewing border with 8 widely spaced teeth, apical tooth largest. Palpal formula: 3:1 or 3:2. *In situ* count. Transverse carina lacking on cervical area; pronotum with median longitudinal carina, laterally with more or less parallel rugulae. Lateral margins of propleura and pronotum evenly curved, without denticle or angle. Mesonotum with 4 denticles, anterior pair longer than posterior; neither promesonotal suture nor metanotal sulcus evident. Antepisternum with low rugae, dorsoanteriorly bound by brief carina; mesopleuron with short ventral carina at mesosomal constriction. Rugae on mesosoma not as broad and coarse as on head; sculpture finer with sparse rugulae. Mesometanotum without well defined longitudinal carinae. Mesosoma laterally with relatively straight anterior pronotal margin; margins of posterior pronotum and mesonotum form convexity interrupted by mesonotal denticles. Metanotum concave; dorsal propodeal face very broadly convex, almost straight, about twice as long as declivitous face. Propodeal dorsum with 2 posterior denticles; base of each propodeal denticle joined to inferior propodeal lobe by vertical carina. Mesopleuron with low anteriorly projecting ventral lobe, just dorsad of mesocoxa. Pronotal-mesopleural suture distinct, terminating dorsally at brief lobe overlapping mesothoracic spiracle; small tubercle present at apparent dorsal end of metapleura. Metapleura and lateral propodeal faces with finely granulose sculpturing, no rugae. Propodeal spiracle prominent, opening directed obliquely laterally. Dorsal propodeal surface forms slightly elevated rectangular surface bordered anterad by transverse carina and laterally by longitudinal carinae that end posterad at propodeal denticles. Convex propodeal lobes present. Petiole slightly pedunculate, node broadly convex, its posterolateral margins angulate and pointing obliquely posterad; low anteroventral lobe present. Petiolar and postpetiolar dorsum rugulose. Postpetiole laterally with convex anterodorsal margin; ventral margin straight, bound at each end by raised triangular margins; dorsal surface with posterolateral ridge ending in rounded lobe. First gastral segment with anterodorsal lobe, a continuous extension of gastral sculpturing partially overlapping

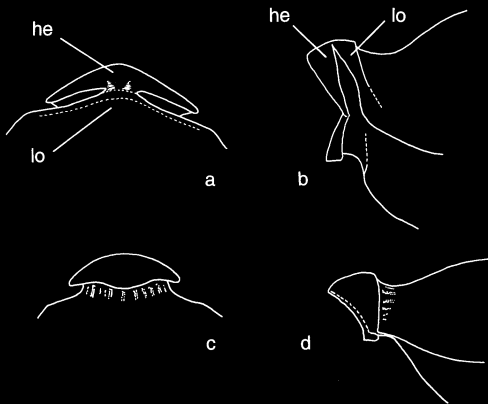


Fig. 4. Helcium and anterodorsal gastral area of *Apterostigma auriculatum* and *Myrmicocrypta buenzlii*. a, dorsal view in *A. auriculatum*; b, lateral view in *A. auriculatum*; c, dorsal view in *M. buenzlii*; d, lateral view in *M. buenzlii*. he = helcium. lo = anterodorsal lobe.

constriction of helcium dorsally (Fig. 4), apex bluntly pointed and base with modest but well-defined transverse concavity. Posterodorsal margin of postpetiole covers most of lobe. Gaster laterally subglobulose, dorsal margin evenly convex and ventral margin sharply convex; tergum of gastral segment I with rugulae forming almost areolate pattern, sternum with rugulae along posteromedian area, fading out towards base; low lateral longitudinal carinae present on tergum. Procoxae mostly smooth except for low rugulae towards apex, no rugulae on meso- and metacoxae. Apex of metacoxa with a sulcus along each side of insertion of trochanter, each sulcus divided into rounded cells. Body without pubescence except on antennal flagella, protibiae and tarsi. Hairs on mesosoma rigid and frequently capitate, those on gaster slender and subdecumbent; head with sparse depressed hairs; vertex and occiput with erect to suberect rigid hairs. Body brown, mandibular masticatory border black.

Queen. Unknown.

Male. Unknown.

Remarks. F. Fernández has supplied additional data about the locality for the Colombian specimen: 'primary forest between Ríos Duda and Guayabero, some kilometres west of the town La Macarena, 350 m.' The collection data for all specimens indicate this species is found in lowland mesic forests. Although only four workers have been found, it is

probably safe to assume that this species is monomorphic, given the small variation in measurements of the studied specimens and the basal position of the group within Attini. Only more derived attines, such as *Acromyrmex* and *Atta*, are polymorphic.

Etymology. The species name is derived from the Greek words for large, *mega*, and head, *kephale*. It alludes to the prominent head.

Discussion

The results of the phylogenetic analysis are shown in Fig. 5. The attine ingroup is divided into a clade formed by *Mycocetopus*, *Myrmicocrypta* and *Apterostigma*, while *Sericomyrmex* is positioned as a sister group to them. *Apterostigma megacephala* has a sister group relationship to the other members of its genus. The fungus ant genera studied here are joined by three synapomorphies: (1) development of a smooth and shiny anterior clypeal margin; (2) presence of lateral carinae along the gastral dorsum; (3) presence of mesonotal denticles. But in some groups at least one of these characters has been lost. The gradual development of a distinct smooth and shiny strip of cuticle along the anterior clypeal border can be traced through these groups. *Blepharidatta*

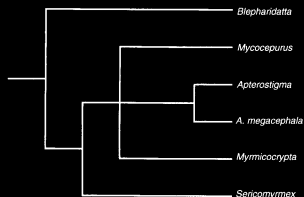


Fig. 5. Strict consensus tree computed from three trees of length 11. CI = 0.73 and RI = 0.63.

brasilienis possesses an anterior lamella, but it is opaque, while *Mycocepurus* has a distinct, though usually inconspicuous, lamella. Some species have traces of shine though, and it is very obvious in *M. tardus* where it is partially smooth and shiny. *Apterostigma*, disregarding *A. megacephala*, can be divided into two clades: one in which the smooth and shiny strip is present, the *pilosum* group, and one in which the strip has been lost, the *auriculatum* group (Lattke, 1997). The presence of lateral carinae along the gastral dorsum is shared by all these attines except *Myrmicocrypta*. All attines considered here have denticles on the mesonotum, with the exception of *Apterostigma*, in which probable vestiges of these can be seen in the prominent triangular lobes of the mesonotal carinae found in a few species of the *auriculatum* group (Lattke, 1997), yet they are retained in *A. megacephala*.

The *Apterostigma* + *Mycocepurus* + *Myrmicocrypta* clade is supported by the loss of the lateral pronotal denticles or angles, and perhaps by the development of the posterolateral clypeal ridge. This ridge stretches from the base of the frontal carinae and extends posterad along the lateral cephalic dorsum. Such a structure is lacking in *B. brasilienis* and its absence in *Apterostigma*, other than *A. megacephala*, is interpreted as a loss.

Apterostigma megacephala shares the following synapomorphies with the rest of *Apterostigma*: (1) each compound eye is partially or totally mounted upon a tubercle; (2) presence of a posterior cephalic ridge or lamella that joins the occipital lobes; (3) an anterodorsal lobe that partially overlaps the helcium of the first gastral tergite. The ocular tubercle is far more developed in *A. megacephala*, being larger than the eye itself, whereas in other *Apterostigma* the eye is always larger. The posterior cephalic ridge is interpreted as homologous to the posterior neck characteristic of other *Apterostigma*. In most *Apterostigma* it is quite developed, forming a lamellar process that completely fuses laterally with the occipital lobes, and forms with them a single structure. The separation between the lobes and the ridge is still evident in *A. megacephala*.

The anterodorsal gastral lobe can only be seen in its entirety by removing the postpetiolar tergite. Unfortunately only the basal and median portions of the anterodorsal gastral lobe are

visible in the *A. megacephala* specimens studied. Dissection of the types was precluded due to each being a unique specimen for each collection. Nevertheless the basal and median structure of the lobe corresponds well to the state in the remaining *Apterostigma* (Fig. 4a,b), and is unlike the other ants studied (Fig. 4c,d). In the other attines dissection was not necessary, as pressing down on the gaster of relaxed specimens permitted viewing of the anterior edge of the first gastral tergite. An additional synapomorphy, considered belatedly, is the reduced palpal formula of *A. megacephala* and other *Apterostigma*. The primitive number in Attini is 4:2 except in two *Acromyrmex* social parasites and in *Apterostigma*, where it is 3:2 (T. Schultz, personal communication; Kusnezov, 1951, 1954). A sister group relationship between *A. megacephala* and the two other *Apterostigma* clades is argued on the basis of these four characters.

Some apomorphies separating all other known *Apterostigma* from *A. megacephala* are: (1) complete loss of the median clypeal seta; (2) loss of distinct mesonotal teeth, represented by two longitudinal carinae, which occasionally are raised into blunt triangles in a few species of the *auriculatum* group; (3) presence of a transverse carina on the cervical area; (4) loss of lateral denticles on the pronotum, sometimes apparently represented as a very inconspicuous swelling on each humeral side; (5) tendency toward loss of the propodeal denticles, which are conserved in a few species of the *auriculatum* group; (6) loss of the posterolateral ridges of the clypeus; (7) transformation of erect and rigid corporal hairs into flexuous and curved, decumbent hairs. Autoapomorphies of *A. megacephala* include: (1) the reduced ommatidia of the compound eyes; (2) the development of spatulate ends on some of the erect corporal hairs; (3) the angulate lobes on the posterolateral petiolar and postpetiolar margins. In *A. megacephala* the median clypeal seta may occasionally be indistinct.

It is concluded that *Apterostigma megacephala* represents a basal species in the *Apterostigma* clade. The objective of this discussion has been to place this new ant within the 'lower' attines, and does not pretend to address the phylogenetic relationships of all attine genera. That will have to await an in-depth study of the entire tribe.

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